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RESEARCH ARTICLE

The effects of rainfall and arthropod abundance on breeding season of insectivorous birds, in a semi-arid neotropical environment

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ABSTRACT. Rainfall in tropical semi-arid areas may act as a reliable cue for timing bird reproduction, since it precedes future food supply. With this in mind, we set-up a study to test the reproductive response of insectivorous bird to arthropod abundance and rainfall patterns. Sampling occurred in a seasonally dry Neotropical forest, in north-eastern Brazil, between October, 2015 and October 2016, at 14-day intervals. We used brood patch to assess reproductive periodicity of insectivorous birds (eight species, 475 captures, 121 patch records). We sampled arthropods to quantify abundance, using biomass and number of individuals (1755 individuals, 15 Orders). Rainfall temporal distribution was analyzed using daily precipitation data. We used a cross-correlation function to test for correlation and time-lags between the covariates under study. Both the number of reproductively-active birds and arthropod abundance were higher in time periods close to the rainy season. Increase in arthropod biomass in the aerial stratum preceded the period of greatest rainfall by one (14 days, r = 0.44) to three sampling periods (0.47). In contrast, the highest proportion of individuals with brood patches occurred after the main rainfall peak, with the strongest relationship occurring after two (0.52) to four (0.50) time lags. Finally, the proportion of individuals with brood patches was positively correlated with aerial stratum arthropod biomass when five time lags were considered (0.55). Our results support the hypothesis of a temporal process involving rainfall, arthropods and reproduction of insectivorous birds in the wet/dry tropics. However, rainfall did not appear to act as a cue for the timing of reproduction, since records indicated higher arthropod biomass before the main rainfall peak. At least occasionally in the study area, insectivorous bird reproduction peaks after food abundance.

KEY WORDS. Brood patch, Caatinga, food-mediated process, insect, reproduction.

INTRODUCTION

In tropical seasonally dry areas there is widespread evidence of links between rainfall, bird breeding phenology and clutch size (Immelmann 1971, Zann et al. 1995, Ahumada 2001, Morrison and Bolger 2002, Cox et al. 2013, Cavalcanti et al. 2016). Such relationships are attributed to the influence of rainfall on both primary productivity and the abundance of arthropods and fruits (Poulin et al. 1992, Lloyd 1999, Schloss et al. 1999, Illera and Díaz 2006, Williams and Middleton 2008), and linked to the role such resources have as important sources of energy to help birds meet the demands of reproduction (Poulin et al. 1993). In this context, rainfall may act as a reliable cue for the timing of reproduction, because of its capacity to predict future food supply, so characterizing a food-mediated process (Illera and Díaz 2006, Dean et al. 2009). However, evidence linking chronology of rainfall, arthropod abundance, and avian reproduction is still preliminary in tropical seasonal environments.

The existence of specific food-mediated processes involving weather, food and bird reproduction were originally proposed for temperate regions, based largely on observed relationships between temperature and avian reproductive periodicity (Skutch 1949, Lack 1954, Ashmole 1963). In temperate climates, high winter bird mortality and high food productivity in the summer result in a food surplus conducive to feeding

young. A similar chronological process may occur in tropical semi-arid forests, where reproduction is linked to rainfall, some bird populations decline during dry periods, and arthropods tend to increase in abundance during the rainfall periods (Illera and Díaz 2006, Dean et al. 2009, Araujo et al. 2017, Silva et al. 2017). However, such traditional views of avian life history and reproductive ecology in seasonal environments have ignored the nature of bird populations in tropical semi-arid regions. In the tropics survival rates are normally high, with little annual variability, but counterbalanced by low annual recruitment and high nest predation rates (Faaborg and Arendt 1995, Martin 1996, Stutchbury and Morton 2001, França et al. 2016). Together, the climatic seasonality, the particularities of life history and a potential food-mediated process in tropical semi-arid areas, can interact to shape breeding phenology of birds (Martin 1995, Morrison and Bolger 2002, Sofaer et al. 2012), producing temporal patterns of reproductive investment that differ from those in both humid tropics and temperate environments.

We explore the relation among rainfall-food-reproduction in an insectivorous bird assemblage in a seasonally dry tropical forest in north-eastern South America (Miles et al. 2006, Pennington et al. 2009). In this region, annual rainfall is both low and restricted to a very few months (Velloso et al. 2002, Prado 2003), and bird reproduction seems to be linked to seasonal climatic patterns (Cavalcanti et al. 2016, Araujo et al. 2017). In environments with similar weather conditions, rainfall is considered the best predictor of arthropod abundance (Poulin et al. 1992, Illera and Díaz 2006, Dean et al. 2009). However, these evaluations generally use broad time-scales to describe the relationship. Given this, we designed a sampling regime with 14-day intervals to evaluate the short-term reproductive responses of the regional avifauna. This made it possible to investigate immediate responses of bird reproduction and arthropod abundance according to rainfall regime. We hypothesize that the temporal distribution of rainfall acts as an indicator of the future availability of food, being used as a short-term signal for avian reproductive activity. Our predictions are that: (1) rainfall will increase future abundance of arthropods and avian investment in reproduction, (2) avian reproductive activity will be linked in an immediate manner to the current abundance of arthropods.

MATERIAL AND METHODS

We conducted the study in Caatinga, a Neotropical dry forest type present in north-eastern Brazil (Miles et al. 2006, Pennington et al. 2009), characterized by high annual temperatures and rainfall concentrated in a four month period (Velloso et al. 2002, Prado 2003). Rains tend to occur during the first half of the year, but their volume and temporal distribution is highly unpredictable within this time period (Prado 2003). In the study region, the annual mean precipitation varied between 500 and 800 mm. The study area is located in a 200 ha fragment of native forest vegetation (5°03'17"S, 37°23'50"W; state of Rio Grande do Norte, Brazil), which lies within a mosaic landscape of small farms and native dry forest patches.

We established a grid of four parallel transects, separated from each other by 100 m. Every 50 m along each transect we placed 10 sampling points, each point with a mist net (18 × 3 m, mesh 16 or 19 mm; 40 sampling points). Each track alternately received nets with a specific mesh width. Between October 2015 and October 2016, we sampled the area by opening mist nets at 05:00 a.m. and keeping them open until 10:00 pm. Sampling occurred every 14 days (27 sampling events), with the aim of capturing the speed of response of the organisms under study. Other studies have reported instances where the reproductive response of tropical birds and the increase in prey abundance occurred 10–14 days after environmental stimuli (Hau et al. 2000, Hau 2001).

Captured birds were marked with coded metal rings provided by the Centro Nacional de Pesquisa para a Conservação das Aves Silvestres (CEMAVE/ICMBio – National Centre for Wild Bird Conservation). These birds were identified and categorized as reproductive by the presence/absence of a brood patch. When present, the brood patch was categorized as: (a) active patch – abdominal region lacking feathers, highly vascularized and with subcutaneous fluid present; or (b) inactive patch – abdominal region lacking feathers, but little vascularized, lacking subcutaneous fluid and with a dry and scaly appearance. For the data analysis we included only records of 'active brood patches'. To quantify reproductive season we examined the active brood patch data and estimate the ratio between the number of individuals with brood patches and the total number of individuals captured during each sampling event. We combined males and females when performing the calculations as the species under study showed no apparent sexual dimorphism, except *Formicivora melanogaster* Pelzeln, 1868, which males also have brood patches. Methods for categorizing reproductive phenology followed those used in previous tropical bird studies (Poulin et al. 1992, Johnson et al. 2012, Cox et al. 2013, Cavalcanti et al. 2016).

Arthropods were sampled at three sites within the grid, all separated by 150 m and on the same days as bird sampling. Three sampling methods were used in each site: windowpane traps, pitfall traps and suction sampling (Gibb and Oseto 2005). Windowpane traps are flight interceptors and were used to sample arthropods flying in the air. These traps consist of a 1 m^2 Perspex plate coupled to a collecting tray beneath. At each sample site we mounted two traps set with bases at 1 m and 2 m above the soil surface. Pitfall traps were used to sample arthropods of the soil surface and leaf litter. Each consisted of a 500 ml bucket buried so that its rim was level with the soil surface. In each one of the three sites, five buckets were placed 10 m one from the other. A suction sampler (design adapted following Stewart and Wright 1995, Buffington and Redak 1998) was used to capture arthropods which usually move on the surface of shrubs and trees. We collected arthropods by sweeping trees and leaves at heights between 0.5 and 2.5 m, using a Blow and Vac machine

(Stihl Ltd, model SH56) converted to produce sucking action. During each sampling event, windowpane and pitfall traps were left open for 48 hours, and the suction-sampling procedure was performed for 10 minutes per sampling point. Collected arthropods were identified to Order, counted and weighed. For weighing, individuals were oven dried at 50°C for 24 hours, then grouped by order and weighed (0.1 mg precision). Since no knowledge existed of the foraging behavior of the focal bird species in the studied seasonal environment, the arthropod sampling methods we chose were exploratory in nature.

To assess the abundance of food resources (arthropods) we used the number and biomass obtained by each sampling method and estimate proportions, using the ratio between abundance at each sampling event and total abundance recorded during the study. We combined data from windowpane traps and suction sampling and treated this as "aerial stratum arthropods". This was done because evidence indicates that, in Neotropical environments, aerial arthropod assemblages tends to suffer marked within-year variation in abundance, whereas abundance of leaf litter arthropods tends to be more constant (Poulin et al. 1992, Ahumada 2001). In addition, we included a variable based on the average of numbers and biomass to represent the combined effect of the abundance variables. In addition, we included a variable based on the average of biomass and numbers (biomass_number) to represent the combined effect of the abundance variables.

Temporal distribution of rainfall was based on daily precipitation data collected with a rainfall gauge located at 10 km from the study site (data available in "CEMADEN – Centro Nacional de Monitoramento e Alertas de Desastres Naturais" – National Centre for Natural Disaster Monitoring and Alerting, http://www.cemaden.gov.br/mapainterativo). We calculated the cumulative precipitation for the 14 days prior to each sampling event, to test the short-term effect of this on the biological processes studied.

We restricted the analysis to eight species of birds whose diets consist of at least 90% invertebrates (diet descriptions: Araujo 2009, Souto 2010), with locally resident populations (V.H. Figueiredo unpublished data), and in which their individuals were recorded at least 20 times: *Cantorchilus longirostris* (Vieillot, 1819), *Casiornis fuscus* Sclater & Salvin, 1873, *Formicivora melanogaster* Pelzeln, 1868, *Hemitriccus margaritaceiventer* (d'Orbigny & Lafresnaye, 1837), *Myiarchus tyrannulus* (Statius Muller, 1776), *Myiopagis viridicata* (Vieillot, 1817), *Polioptila plumbea* (Gmelin, 1788) and *Tolmomyias flaviventris* (Wied, 1831) (Nomenclature follows South American Classification Committee (SACC).We excluded those species who obtained their food by excavation (Picidae and Dendrocolaptidae), as we did not have samples of their food types. For arthropods, we analysed only those Orders shown by previous investigations to be part of the diet of the eight studied species (Araujo 2009). In consequence, the following Taxa were analysed: Coleoptera, Hemiptera, Hymenoptera, Isoptera (Infraorder), Mantodea, Orthoptera and Araneae.

We used a Cross-correlation Function (CCF) to test for correlations and time lags between accumulated precipitation, arthropod abundance and brood patch records. CCF was used to correlate two time series (y and x) to enable the effects of different time lags of the y-variable to be checked against the x-variable. Negative lags indicate that y-series values are related to previous x-series values, while positive lags indicate that y-series values precede y-series values (Brockwell and Davis 1991). Statistical analyses were performed using R, version 3.4.1 (R Core Team 2016), using the package tseries.

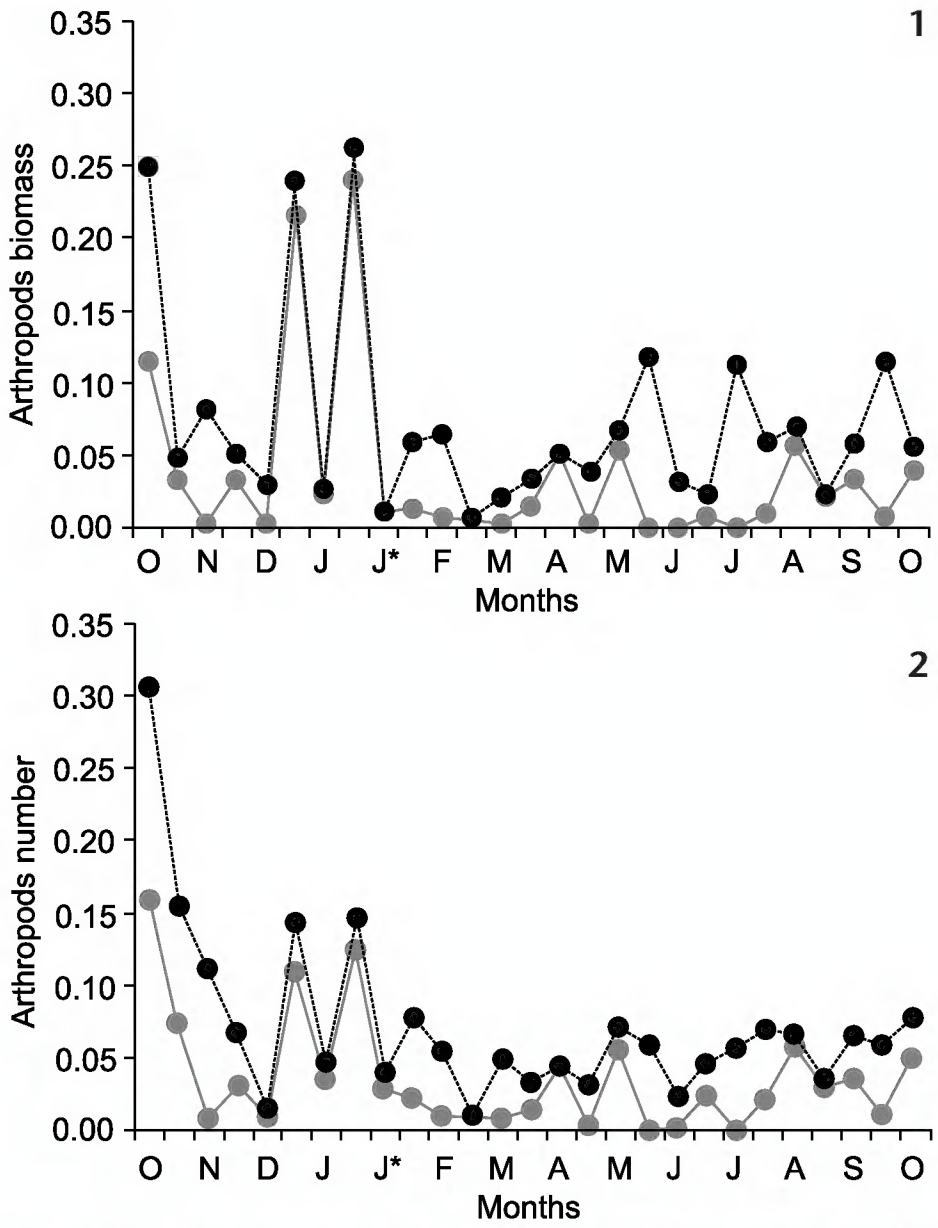
RESULTS

During the study, rains occurred mostly between January and June, with annual precipitation (313 mm) below the regional mean. In arthropod traps we recorded 1755 individuals and identified 15 orders. From these, 1293 individuals were from the seven Orders considered in the analyses (Table 1). Records by trap type were distributed as follows: 384 individuals by windowpane trap; 125 by suction sampler; 784 by pitfall traps. Arthropod abundance (numbers and biomass) showed high within-year variation regardless of the capture substrate type (Figs 1–2). However, biomass records showed abundance peaks that exceeded the individuals peaks, especially between January and February (Figs 1–2). We recorded 73 bird species of which eight met the pre-established criteria to be included in the study. For these focal species, we recorded 475 capture-recaptures and 121 brood patch.

Table 1. Abundance of arthropods from 27 sampling events, based on three sampling procedures (windowpane, pitfall, suction). Values correspond to the number of individuals and biomass (dry weight in grams). Data recorded between October 2015 and October 2016, with 14-day intervals, in an area of Neotropical seasonally dry forest in northeastern Brazil.

Taxon	Windowpane	Pitfall	Suction
Insecta			
Coleoptera	208 (0.786)	215 (0.592)	30 (0.108)
Hemiptera	2 (0.033)	0 (0.00)	0 (0.00)
Hymenoptera	119 (0.325)	431 (2.439)	18 (0.023)
Isoptera (Infraordem)	37 (0.619)	1 (0.002)	0 (0.00)
Mantodea	1 (0.001)	0 (0.00)	0 (0.00)
Orthoptera	5 (0.004)	26 (0.151)	50 (0.128)
Arachnida			
Araneae	12 (0.023)	110 (0.357)	21 (0.014)
Larvae	0 (0.00)	1 (0.001)	6 (0.013)

Aerial stratum arthropod biomass was positively correlated with rainfall distribution, preceding it by one to three time units (time unit = 14 days; Table 2, Fig. 3). In contrast, the highest proportion of individuals with brood patches occurred after more intense periods of rain, and the strongest relation was found when two or four time lags were considered (Table 2, Fig. 4).



Figures 1–2. (1) Biomass and (2) number of arthropods recorded during 27 sampling events. Solid lines represent the aerial arthropods (windowpane trap and suction sampler), while dashed lines show terrestrial arthropod (pitfall trap). Data recorded between October 2015 and October 2016, with 14-day intervals, in an area of seasonally dry Neotropical forest, in northeastern Brazil. The abundance (biomass and number) were converted to proportion using the ratio between abundance at each sampling event and total abundance during the study. *In one month, we had three, instead of two, monthly samplings as a result of the 14-day interval between samples.

Finally, the proportion of individuals with brood patches was positively correlated with biomass of aerial stratum arthropods, when considering five time lags for brood patches in relation to arthropods abundance (Table 2, Fig. 5). The time lag of this last correlation was equivalent to the sum of response times between arthropods and precipitation (strongest correlation occurring with three time units), and between brood patch and precipitation (strongest correlation with two time units). The number of arthropods in the aerial stratum and the two terrestrial arthropod abundance variables were not significantly correlated with precipitation or presence of brood patches (Table 2). Arthropod biomass was always associated with stronger correlations than any variable that combined arthropod numbers and biomass.

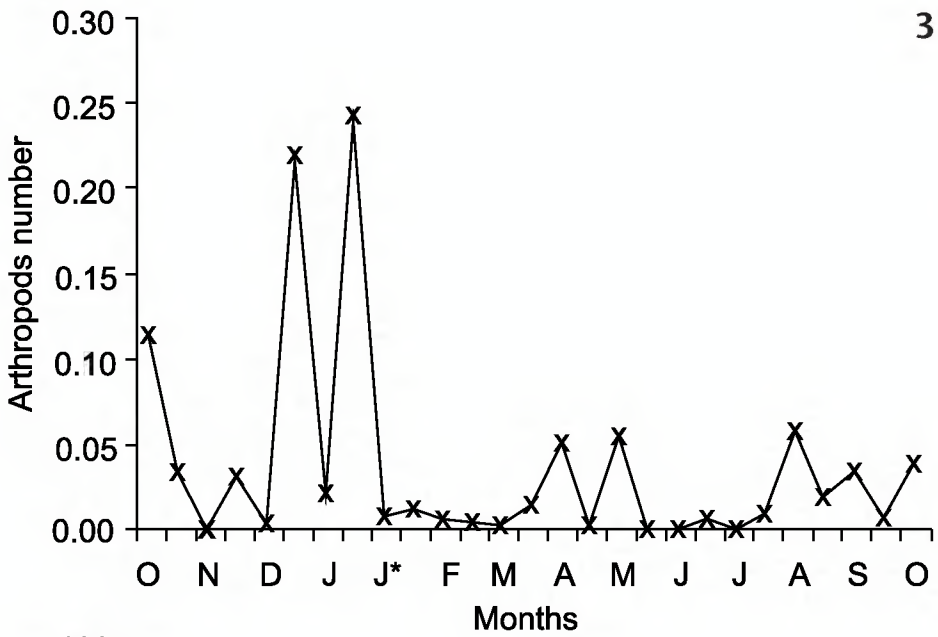
Table 2. Correlation coefficients (r) and time-lags of the cross-correlation function that had $p < 0.05$. Accumulated precipitation, arthropods abundance (number and biomass), and the proportion of individuals with active brood patches were correlated with each other. Each lag unit corresponded to a sample interval of 14 days, with up to six lags considered in each direction.

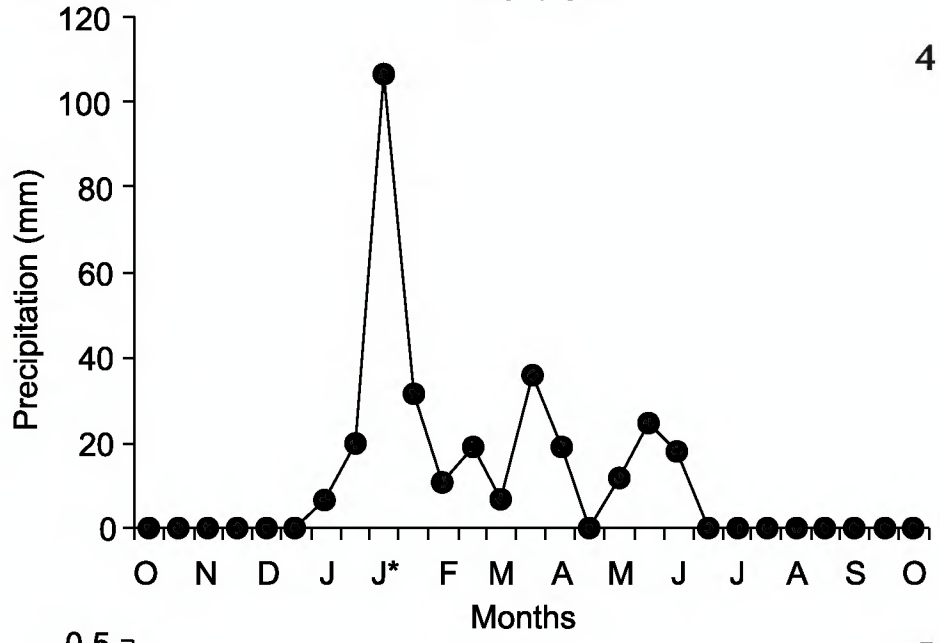
Covariables		r	lag
X	Y		
Accumulated precipitation	Biomass (aerial stratum)	0.436	1
		0.465	3
Accumulated precipitation	Biomass (pitfall)	–	–
Accumulated precipitation	Number (aerial stratum)	–	–
Accumulated precipitation	Number (pitfall)	–	–
Accumulated precipitation	Biomass number (aerial stratum)	0.394	3
Accumulated precipitation	Biomass number (pitfall)	–	–
Biomass (aerial stratum)	Brood patch	0.549	-5
		0.463	-6
Biomass (pitfall)	Brood patch	–	–
Number (aerial stratum)	Brood patch	–	–
Number (pitfall)	Brood patch	–	–
Biomass_number (aerial stratum)	Brood patch	0.489	-5
		0.400	-6
Biomass_number (pitfall)	Brood patch	–	–
Accumulated precipitation	Brood patch	0.462	0
		0.430	-1
		0.521	-2
		0.382	-3
		0.501	-4

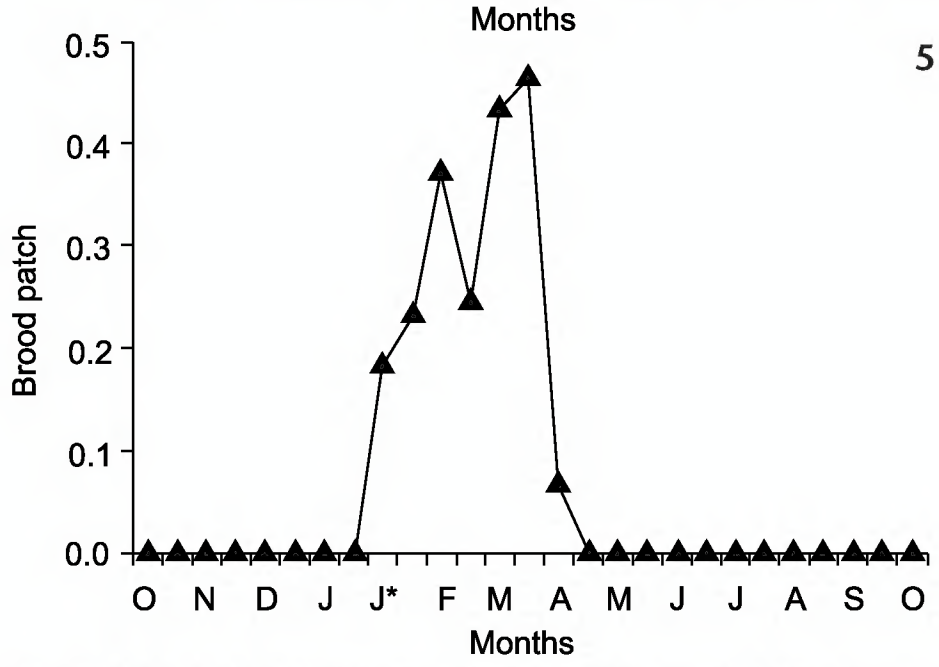
The two largest aerial arthropod biomass peaks occurred in final third of December and January, when in 28 days we captured 43% of the total aerial arthropod biomass recorded during the study. The highest accumulative precipitation occurred shortly after, between the end of January and February, when 55% of the total rainfall volume recorded fell in 39 days (Fig. 4). Brood patches were present in an 84 day period between January and April, with highest activity between late February and early April over 42 days (Fig. 5).

DISCUSSION

Our results support the hypothesis that there is a causative process involving precipitation patterns, food resources abundance (arthropod) and the reproductive period of insectivorous birds in the seasonally dry tropics (Frith and Frith 2005, Illera and Díaz 2006, Dean et al. 2009). A relationship between timing of Caatinga dry forest bird reproduction and the rainy season has been reported by other studies (Cavalcanti et al. 2016, Araujo et al. 2017). In the current study, reproduction was observed to occur in two-month lags after the peak of the rainfall period (four time lags). Such lags are generally considered to occur as part of a mechanism that involves food supply abundance, in







Figures 3–5. (3) Aerial arthropod biomass, (4) accumulated precipitation and (5) active brood patches, during 27 sampling events. Data recorded between October 2015 and October 2016, with 14-day intervals, in an area of seasonally dry Neotropical forest in northeastern Brazil. The biomass were converted to proportion using the ratio between abundance at each sampling event and total abundance during the study. Brood patch was converted to proportion using the ratio between individuals with brood patches and total individuals captured during a sampling event. *In one month, we had three, instead of two, monthly samplings as a result of the 14-day interval between samples.

this case, of arthropods (Frith and Frith 2005, Illera and Díaz 2006). Our results also indicate high annual variation in arthropod abundance (especially for aerial arthropods), providing support for the premise that this is associated with within-year rainfall seasonality.

However, we found no evidence for the food-mediated process described in previous studies, where the rainfall is used by birds as a cue to future food availability and so regulates the timing of breeding in a way that deals effectively with the temporal unpredictability of this resource (Hau 2001, Illera and Díaz 2006). Our data recorded peaks of arthropod abundance preceding the most intense rainfall. Reproductive responses triggered directly by increases in food abundance have been recorded during an experimental study of gonadal development in tropical birds (O'Brien and Hau 2005). Our findings do not rule out the importance of rain as a predictor of food supply for bird reproduction in the semi-arid environment studied. This is mainly because we do not have a data set that is long enough to show the frequency with which the observed process repeats itself in the study area. On the other hand, our results are a warning that the mechanism that links rain, arthropod abundance, and breeding patterns in the studied birds may not be as deterministic as previously believed.

It is possible that the studied birds used the short period of food surplus to gain enough energy reserves and then reproduce, interrupting the long period of food restriction imposed by the dry period. This approach runs against the prediction that food surplus in seasonal/unpredictable environments is used to feed nestlings and fledglings, reducing the impact of severe periods on their survival (Lack 1954, Nager and Noordwijk 1995, Houston 2013). On the other hand, food availability during reproductive timing competes with nest predation in terms of direct impact on bird reproductive success in the semi-arid tropics (Stutchbury and Morton 2001, França et al. 2016), and seems to determine bird reproductive periodicity (Martin 1995, 1996). The pattern detected here seems to be repeated in other Neotropical dry forest areas where, at least partially, a higher abundance of arthropods has been recorded immediately before to rainfall peaks or preceding insectivorous bird reproductive activity periods (Poulin et al. 1992, Araujo et al. 2017).

We suggest here the existence of alternative mechanisms to explain the reproductive timing of birds in dry tropical forests, such that the birds use food abundance rather than rainfall as a proximate cue to adjust the timing of reproduction. Although, explanatory power of the data was still limited by the temporal nature of this research and by the lack of information on other aspects of bird reproduction. For example, relationships between reproductive phenology and nest predation have yet to be clarified, as have the potential effects of factors that covary with food abundance or rainfall period (Morrison and Bolger 2002, Sofaer et al. 2012). Regardless of this, we detected a distinct chronological relation between rainfall, arthropods abundance and bird reproduction in the studied area, and this empowers future research.

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LITERATURE CITED

Ahumada JA (2001) Comparison of the reproductive biology of two neotropical wrens in an unpredictable environment in northeastern Colombia. Auk 118: 191–210.

Araujo HFP (2009) Amostragem, estimativa de riqueza de espécies e variação temporal na diversidade, dieta e reprodução de aves em área de Caatinga. PhD thesis, Universidade Federal da Paraíba, João Pessoa, Paraíba. Available online at: https://repositorio.ufpb.br/jspui/handle/tede/7939

Araujo HFP, Vieira-Filho AH, Barbosa MRDV, Diniz-Filho JAF, Silva JMC (2017) Passerine phenology in the largest tropical dry forest of South America: effects of climate and resource availability. Emu 117: 78–91.

Ashmole NP (1963) The regulation of numbers of Tropical Oceanic Birds. Ibis 103: 458–473.

Brockwell PJ, Davis RA (1991) Time series: theory and methods. Springer Verlag, New York, 520 pp.

Buffington ML, Redak RA (1998) A comparison of vacuum sampling versus sweep-netting for arthropod biodiversity measurements in California coastal sage Scrub. Journal of Insect Conservation 2: 99–106.

Cavalcanti LM, Paiva LV, França LF (2016) Effects of rainfall on bird reproduction in a semi-arid Neotropical region. Zoologia 33: e20160018.

Cox DTC, Brandt MJ, Mcgregor R, Ottosson U, Stevens MC, Cresswell W (2013) The seasonality of breeding in savannah birds of West Africa assessed from brood patch and juvenile occurrence. Journal of Ornithology 154: 671–683.

Dean WRJ, Barnard P, Anderson MD (2009) When to stay, when to go: trade-offs for southern African arid-zone birds in times of drought. South African Journal of Science 105: 24–28.

Faaborg J, Arendt WJ (1995) Survival rates of Puerto Rican birds: are islands really that different? Auk 112: 503–507.

Figueiredo VH (2016) Período de ocorrência de aves migratórias em uma floresta tropical seca. MsC thesis, Universidade Federal Rural do Semi-Árido, Mossoró, Rio Grande do Norte. Available online at: https://repositorio.ufersa.edu.br/bitstream/prefix/2192/1/HelyaMSS_DISSERT.pdf

França LF, Silva CM, Paiva LV (2016) Effects of intrinsic and time-specific factors on daily nest survival of birds in a semi-arid area of South America (Caatinga). Revista Brasileira de Ornitologia 24: 228–234.

Frith CB, Frith DW (2005) A long-term banding study in upland tropical rainforest, Paluma Range, north-eastern Queensland with notes on breeding. Corella 29: 25–48.

Gibb T, Oseto C (2006) Arthropod Collection and Identification: Laboratory and Field Techniques. Elsevier Academic Press, Amsterdam, 336 pp.

Hau M (2001) Timing of Breeding in Variable Environments: Tropical Birds as Model Systems. Hormones and Behavior 40: 281–290.

Hau M, Wikelski M, Wingfield JC (2000) Visual and nutritional food cues fine tune timing of reproduction in a neotropical rainforest bird. Journal of Experimental Zoology 286: 494–504.

Houston WA (2013) Breeding cues in a wetland dependent Australian passerine of the seasonally wet-dry tropics. Austral Ecology 38: 617–626.

Illera JC, Díaz M (2006) Reproduction in an endemic bird of a semiarid island: A food-mediated process. Journal of Avian Biology 37: 447–456.

Immelmann K (1971) Ecological aspects of periodic reproduction. In: DS Donalds, JR King (Eds) Avian biology. Academic Press INC, London, vol. 1, 341–389.

Johnson EI, Stouffer PC, Bierregaard RO Jr (2012) The phenology of molting, breeding and their overlap in central Amazonian birds. Journal of Avian Biology 43: 141–154.

Lack D (1954) The natural regulation of animal numbers. The Clarendon Press, Oxford, 343 pp.

Lloyd P (1999) Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. Ibis 141: 637–643.

Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65: 101–127.

Martin TE (1996) Life history evolution in tropical and south temperate birds: what do we really know? Journal of Avian Biology 27: 263–272.

Miles L, Newton AC, Defries RS, Ravilious C, May I, Blyth S, Kapos V, Gordon JE (2006) A global overview of the conservation status of tropical dry forests. Journal of Biogeography 33: 491–505.

Morrison SA, Bolger DT (2002) Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. Oecologia 133: 315–324.

Nager RG, Van Noordwijk AJ (1995) Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. The American Naturalist 146: 454–474.

O'Brien S, Hau M (2005) Food cues and gonadal development in Neotropical spotted antbirds (*Hylophylax naevioides*). Journal of Ornithology 146: 332–337.

Pennington RT, Lavin M, Oliveira-Filho A (2009) Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. Annual Review of Ecology, Evolution, and Systematics 40: 437–457.

Poulin B, Lefebvre G, Mcneil R (1992) Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73: 2295–2309.

Poulin B, Lefebvre G, Mcneil R (1993) Variations in bird abundance in tropical arid and semiarid habitats. Ibis 135: 432–441.

Prado DE (2003) As Caatingas da América do Sul. In: Leal IR, Tabarelli M, Silva JMC (Eds) Ecologia e conservação da Caatinga. Editora Universitária da UFPR, Recife, 03–74.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org

Schloss AL, Kicklighter DW, Kaduk J, Wittenberg U (1999) Comparing global models of terrestrial net primary productivity (NPP): comparison of NPP to climate and the Normalized Difference Vegetation Index (NDVI). Global Change Biology 5: 25–34.

Silva CCO, Pichorim M, Moura PTS, França LF (2017) Seasonality in abundance and detection bias of birds in a tropical dry forest in north-eastern South America. Journal of Tropical Ecology 33: 365–378.

Skutch AF (1949) Do tropical birds rear as many young as they can nourish? Ibis 91: 430–455.

Sofaer HR, Sillett TS, Peluc SI, Morrison SA, Ghalambor CK (2012) Differential effects of food availability and nest predation risk on avian reproductive strategies. Behavioral Ecology 24: 698–707.

Souto GHBO (2010) Ecologia alimentar de aves insetívoras de um fragmento de mata decídua do extremo norte da Mata Atlântica. Msc Thesis, Universidade Federal do Rio Grande do Norte, Natal, Rio Grande do Norte. Availble online at: https://repositorio.ufrn.br/jspui/handle/123456789/13063

Stewart AJ, Wright AF (1995) A new inexpensive suction apparatus for sampling arthropods in grassland. Ecological Entomology 20: 98–102.

Stutchbury BJM, Morton ES (2001) Behavioral ecology of tropical birds. Academic Press, San Diego, 165 pp.

Velloso AL, Sampaio EVSB, Pareyn FGC (2002) Ecorregiões propostas para o Bioma Caatinga. Associação Plantas do Nordeste, Instituto de Conservação Ambiental, The Nature Conservancy do Brasil, Recife, 75 pp.

Williams SE, Middleton J (2008) Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change. Diversity and Distributions 14: 69–77.

Zann RA, Morton SR, Jones KR, Burley NT (1995) The timing of breeding by zebra finches in relation to rainfall in central Australia. Emu 95: 208–222.

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